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Reproductive strategies in the squids of the family Ommastrephidae (preliminary report)

Ch.M.NIGMATULLIN and V.V.LAPTIKHOVSKY

Atlantic Research Institute of Fisheries and Oceanography, 5 Dm. Donskoy Str., Kaliningrad 236000 Russia

The data are presented and analyzed on mature egg size, potential and relative fecundity, coefficient of vitelline oocytes, and peculiarities of maturation of female reproductive system in 17 species of all eleven genera of the family Ommastrephidae. Two main reproductive strategies are outlined: offshore (*Illex* type, four subtypes) and oceanic (*Sthenoteuthis* type, three subtypes) ones. The former is characteristic of relatively primitive subfamilies, the latter — of more evolutionarily advanced ones; some evolutionary vectors are observed in both strategies. Enhanced K-strategy is peculiar in the shelf-slope species and pronounced r-strategy — in the oceanic ones. There are considerable differences between adult females of the 1st and 2nd types in potential fecundity (in the 1st type it is 5-10 times lower than in the 2nd) and relative fecundity (3-7 times) as well as in the relative daily weight growth rates, but the reproductive investment (egg weight relative to female's body weight increase from the beginning of vitellogenesis up to early spawning state) is similar in both types, about 50-60%. The increase in fecundity during the penetration of a group into epipelagic biotopes of the open ocean is the general rule at least for squids and scombroid fishes.

Репродуктивные стратегии кальмаров семейства Ommastrephidae (предварительное сообщение)

Ч.М.НИГМАТУЛЛИН, В.В.ЛАПТИХОВСКИЙ

Атлантический научно-исследовательский институт рыбного хозяйства и океанографии, Калининград 236000, Дм. Донского 5

Для 17 видов всех 11 родов семейства Ommastrephidae получены и проанализированы данные о размере зрелых яиц, потенциальной и относительной плодовитости, доле (коэффициенте) вителлиновых ооцитов и закономерностях хода созревания самок. Выделены две основные репродуктивные стратегии: прибрежная (тип *Illex* с 4 подтипами) и океаническая (тип *Sthenoteuthis* с 3 подтипами). Первый тип характерен для относительно примитивных подсемейств, второй для продвинутых; в пределах каждого выделяются эволюционные векторы. Для шельфово-склоновых видов характерно относительное преобладание черт К-стратегии, для океанических — r-стратегии. При значительных различиях самок 1 и 2 типов по потенциальной (у первого в 5-10 раз ниже, чем у второго) и относительной (в 3-7 раз) плодовитости и темпам весового прироста, репродуктивный вклад (вес яиц по отношению к увеличению веса тела за период от начала вителлогенеза до начала нереста) для обоих типов сходен, около 50-60%. Увеличение плодовитости в ходе освоения эпипелагиали открытого океана — общая черта репродуктивной стратегии кальмаров и скомброидных рыб.

A number of mutually determined reproductive features of animals (reproductive strategy), reflect in integral manner many peculiarities of the ecosystem, the position of population in the biotic structure, and the influence of the controlling abiotic factors on the reproduction. Nektonic ommastrephid squids penetrated in the process of adaptive radiation into almost all ecologically important centers and climatic zones of the World Ocean, where they became dominating species. Their life cycles passes in different types of communities, thus they are an appropriate object for the analysis of ecological implication of their reproductive strategies. There are only a few works on fecundity, egg size and peculiarities of spawning in several

species of the family [Petrov, 1977; Okutani, 1983; O'Dor, 1983; Harman et al., 1989; Nigmatullin, Laptikhovsky, 1990; Laptikhovsky, Nigmatullin, 1992, 1993; Laptikhovsky, Zorikova, 1992], but general patterns of reproductive strategies are still unknown.

The reproductive characteristics of female squids were studied in 442 specimens belonging to 17 species of all 11 genera of this family. The methods of study have been described earlier [Nigmatullin et al., 1981; Nigmatullin, Laptikhovsky, 1990; Laptikhovsky, Nigmatullin, 1992, 1993]. All species are monocyclic with asynchronous oocyte development [Takahasi, Yahata, 1973; Burukovsky et al., 1977], their life duration usually does not exceed one year except in *Martialia hyadesi* and large individuals (mantle length more than 70-80 cm) of *Dosidicus gigas* and *Ommastrephes bartramii* [Arkhipkin,1989; A.I.Arkhipkin and A.B.Mikheev, pers. comm.]. All have a planktonic rhynchoteuthion larva with mortality at this stage more than 95% [Okutani, Watanabe, 1983; Laptikhovsky et al., 1993]. Specimens of *Illex argentinus, Todarodes angolensis, D. gigas* and two species of *Sthenoteuthis* consitute the bulk (more than 80%) of the materials and were used as model species. Literature data on *Todarodes pacificus* [Okutani, 1983] and partially *Illex illecebrosus* [O'Dor, 1983] were also used. Most of our conclusions are based on the data on these species. In the model species, the animals at 1-6 (*I.argentinus* — 1-7) maturity stages according to Nigmatullin's scale [1989] have been studied. To study the reproductive strategy pattern, we used:

1. Ripe egg diameter (ED); to randomize the selection of the diameter measurements, the micrometer was placed in a horizontal position in the eyepiece and the diameter parallel to graduation of the micrometer was measured in 50 eggs).

2. Potential fecundity (PF); it was calculated as a sum of total oocyte number in the gonad and egg number in both oviducts; this stock remains constant since immaturity (end of 2nd maturity stage) and up to the beginning of egg release during spawning; the actual fecundity is 60-80% PF, other oocytes are resorbed in spent females [Nigmatullin, Laptikhovsky, 1990; Laptikhovsky, Nigmatullin, 1992, 1993; Laptikhovsky, Zorikova, 1992].

3. Relative fecundity (RF); it is the ratio of PF to body weight in adult squids.

4. Coefficient of vitelline oocytes (CVO); it is the ratio of sum of the vitelline oocytes in gonad and ripe eggs in oviducts to PF in prespawning females; it shows the share of oocytes simultaneously drawn into vitellogenesis and, therefore, reflects the peculiarities of the yolk oocytes stock replenishment and of the spawning.

5. Peculiarities of maturation of reproductive system, particularly the correlation between growth rates of ovary and accessory glands, the duration of ovary maturation in relation to duration of ontogenesis.

The following types of reproductive strategies were revealed:

1. Offshore strategy (type *Illex*). The maturation of the ovary is relatively long, gradual and forestalls the maturation of the accessory glands. ED is from 0.7-0.9 to 2.2 mm, in most species 0.9-1.2 mm; the egg weight 0.4-0.65 mg. PF increases with body size growth; it is in different species 0.05-1.2 million eggs. RF in all species is about 500-1500 egg/g, except *I. coindeti* whose RF may attain 2500 egg/g including the smallest eggs. CVO is 25-60% and decreases in species having large ripe eggs. Spawning lasts about 1-1.5 months (*Illex*), it is intermittent and with decreasing intensivity: after the end of the first period of egg accumulation in oviducts, the first egg mass or several egg masses are laid (these comprise 30-50% of actual fecundity); next masses comprise 15-5% (in *I.argentinus* the actual fecundity is about 70% of PF). During spawning time the feeding activity initially declines, then ceases, the body weight decreases up to 30-40% of the prespawning weight. Spawning occurs usually in offshore side of western and eastern boundary currents, near the bottom of the shelf and continental slope; in several populations also in the vicinity of oceanic islands and underwater mountains. This strategy is typical for slope-shelf and neritic-oceanic species of Illicinae, Todaropsinae and Todarodinae.

1.1 *Illex* spp., *Todarodes pacificus*. ED — 0.7-0.9 mm, PF — 0.05-0.8 million eggs.

1.2 *Illex argentinus* (slope-oceanic winter spawning group), *Todarodes angolensis, T.filippovae, T.sagittatus* (populations living off North-West Africa, in the Cape Blanc region), *Nototodarus* spp., *Todaropsis eblanae* — ED — 1-1.3 mm, PF — 0.04-1.2 million eggs.

1.3 *Martialia hyadesi*. ED — 1.55 mm, PF — 0.25-0.6 million eggs.

1.4 *Todarodes sagittatus* (populations inhabiting the North Atlantic and the Mediterranean). ED — 2.2-2.4 mm, PF is more than 2 million eggs; type of spawning may be specific with declined share of potential fecundity that have being spawned.

2. Oceanic strategy (*Sthenoteuthis* type). Ovary maturation occurs avalanche-like, rather rapidly and lags behind maturation of the accessory gland. ED — 0.7-1 mm, in most species — 0.75-0.85 mm, egg weight 0.2-0.24 mg. PF increases with the body size growth and in different species varies from 0.1 to 22 million eggs, RF is 2000-7000 egg/g, CVO is about 3-15%, mainly less than 10%. Spawning lasts for several months (*Sthenoteuthis*); it is intermittent and multiportional, with relatively stable intensity (egg

numbers in the first and following egg masses are comparable). During spawning, active feeding is maintained and significant somatic growth occurs. Spawning is not connected with the bottom (the only exception are large-sized slope intraspecific groups of both species of *Ornithoteuthis*) and occurs in epipelagic zone, usually at offshore (oceanic) side of western and eastern boundary currents (California, Peru, Falkland, Brazil, Canary Currents) and in open waters. This strategy was revealed in neritic-oceanic Ornithoteuthinae and *Dosidicus,* and in oceanic Ommastrephinae.

2.1 CVO is usually more than 10%: *Ornithoteuthis* spp. (PF 0.05-0.7 million eggs) and *Dosidicus gigas* (PF 0.3-13 million eggs); RF is 1500-3500 egg/g.

2.2 CVO is usually less than 10%

2.2.1 *Sthenoteuthis* spp., *Ommastrephes bartramii* and probably *Eucleoteuthis luminosa.* PF 0.4-22 million eggs, RF 3000-7000 egg/g, CVO less than 10%.

2.2.2 *Hyaloteuthis pelagica* and *Sthenoteuthis oualaniensis* dwarf form (without dorsal photophore). PF about 0.1 million eggs, RF 6000-7000 egg/g, CVO 3-5%.

The significant differences between the squids of types 1 and 2 were revealed in the male reproductive strategies too [Nigmatullin, Sabirov, 1987].

The first type of reproductive strategies is characteristic of relatively primitive subfamilies, the second one — for more evolutionarily advanced. The transition from the first to the second type corresponds to the main direction of evolution of the family: the environmental alteration from initial slope-shelf biotopes to oceanic epipelagic ones [Nigmatullin, 1979]. Ancestral reproductive features mostly correspond to the group 1.1. Futhermore within each type of reproductive strategy, the rows 1.1 — 1.2 — 1.3 and 1.4 on the one hand, and 1.1 — 2.1 — 2.2.1 and 2.2.2 on other hand appear to be the evolutionary vectors from primitive to more advanced forms. Evolution of ommastrephids in the shelf and slope ecosystems and, further, in areas of underwater mountain occurrence (the row 1.1 — 1.2 — 1.3 — 1.4), where predictability of the ecosystem variability is relatively high, has a tendency towards K-strategy (increase in the egg size with the retention of moderate level of fecundity). During the penetration into oceanic pelagic waters (1.1 — 2.1 — 2.2.1 and 2.2.2) with low predictability of environmental variations causing strong increase in the mortality, the increase in PF occurred with the retention of initial egg size that is minimal possible for cephalopods. *Ornithoteutnis* and *Dosidicus* occupied the most oceanic "position" among neritic-oceanic forms and, therefore, are characterized by features (values of PF, CVO, the peculiarities of the spawning biotope) intermediate between type 1 and oceanic pelagic ommastrephids such as *Sthenoteuthis.* All these features require the change of spawning type and mode of life with a transition to more expressed r-strategy and with a need of active feeding in the spawning period; the latter circumstance is caused by necessity of additional energetic sources for extra generative production.

Strengthening of K-strategy features in the shelf-slope species and r-strategy features in the oceanic species occurs within the r part of the r-K continuum of cephalopods. Nevertheless in some species of each type (*Illex, Ornithoteuthis, Dosidicus* and *Sthenoteuthis*) one can observe some simultaneous and far-reaching microevolutionary tendencies towards r-strategy (nanisation and shortening of the life cycle with early maturation and increase of RF) as well as towards K-strategy (size increase with retention of one-year life cycle owing to high growth rates at early ontogenetic stages, subsequently going out of the control of common predators; in some cases also the increase of the egg size).

There are great differences in PF (by a factor of 5-10) and RF (by a factor of 3-7) between adult females of the same size belonging to 1st and 2nd types of the reproductive strategies. What this means is that significant differences in reproductive effort are probable. Nevertheless, following the different relative daily weight growth rates in mature females, (about 0.5-1.0% per day in *I.argentinus* [Arkhipkin, 1990] and 1.8-2.5% per day in *S.pteropus* [Arkhipkin, Mikheev, 1992]), we can estimate the "reproductive investment" expressed as total weight of eggs produced by a female in relation to its body weight increase from beginning of the vitellogenesis up to the full maturity or to early spawning stage. In representatives of two alternative reproductive strategies these values turned out to be similar: about 50-60%. This probably reflects the similarity in reproductive efforts in both strategies. This fact corresponds to the hypothesis that the reproductive effort does not depend on the reproductive strategy but has an evolutionarily stable value [review: Kasyanov, 1989].

We suppose that the increase in fecundity during the penetration of a group into the biotopes of epipelagic layers of the open ocean is the general rule at least for squids and scombroid fishes [Alexeev, Alexeeva, 1981]. However, in squids this process shows itself more clearly due to the necessity to spawn all reserve of ontogenic fecundity in a single reproductive season in contrast to polycyclic fishes.

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